THE BEE-FLIES *(BOMBYLIIDÆ)* IN THEIR RELATIONS TO FLOWERS.

By S. Graenicher.

The *Bombyliidæ* represent highly specialized forms of the dipterous type, insects that are of importance to many of our flowers as regular and efficient pollen-distributors. Concerning their relations to flowers in general, as also to certain types of flowers, the results obtained from observations carried on in this country are in some respects quite at variance with those reported from European countries.

In Knuth's Handbook of flower pollination, the most recent and most important of its kind we meet in Vol. I, pp. 182 and 183 (Engl. translation) with the following statements: "Although the family of the bee-flies (*Bombyliidæ*) includes short tongued forms (*Lomatia*, *Anthrax*, *Argyromœba*) with a decided preference for flowers with exposed nectar, the species of *Bombylius*, *Systœchus* and *Dischistus* are provided with a long proboscis, with which they suck nectar as they hover."

"On the other hand social flowers are much less convenient for sucking while hovering, and are consequently only very rarely visited by these insects."

"Their preference for red, violet and blue is so remarkable that they were observed on three times as many flowers of these colors as on white or yellow ones. (Mueller, Alpenblumen 515)."

In the foregoing three points are involved: First, the preference of short-tongued species for flowers with exposed nectar; second, the relations to social flowers; and third, the theory of color preference as set forth by Herman Mueller.

The following discussion is based on a comparison of observations made by the author in Milwaukee Co. with the very extensive observations of Robertson[1] in Carlinville, Macoupin Co. in southern Illinois.

COLOR PREFERENCE.

According to Mueller's theory, as referred to above, these flies show a most decided preference for red, purple (or violet)

1) Cited in Knuth's Handbuch d. Bluetenbiologie. Vol. III. part 2, pp. 374-376.

and blue flowers; but the evidence furnished by the visits of the following 9 more or less common species of bee-flies does not agree at all with the theory in question.

1. **Anthrax alternata** Say.

Flowers visited: *Solidago juncea.*[2] Yellow.
Solidago canadensis. Yellow.
Anthemis Cotula. White.
Arctium Lappa. Purple.
Parnassia caroliniana. White.
Rhus glabra. Yellowish.
Verbena hastata. Blue.
Angelica atropurpurea. White.
Pastinaca sativa. Yellow.
Sium cicutæfolium. White.
Oxypolis rigidior. White.
Cicuta maculata. White.

Alltogether for the 12 flowers:
White and yellow 83.3%
Red, purple and blue 16.7%

2. **Anthrax halcyon** Say.

Flowers visited: *Aster puniceus.* Blue.
Eupatorium perfoliatum. White.
Eupatorium purpureum. Purple.
Solidago juncea. Yellow.
Solidago canadensis. Yellow.
Solidago graminifolia. Yellow.
Rudbeckia laciniata. Yellow.
Helianthus strumosus. Yellow.
Helenium autumnale. Yellow.

Alltogether for the 9 flowers:
White and yellow 77.8%.
Red, purple and blue 22.2%.

3. **Bombylius fulvibasis** Macq. (*atriceps* Loew).

Flowers visited: *Allium canadense.* Reddish.
Smilacina racemosa. White.
Viburnum dentatum. White.
Stellaria longipes. White.

2) Nomenclature according to Gray's Manual of Botany, 7th edit. (1908)

Alltogether for the 4 flowers:

White 75.0%.
Red 25.0%.

4. **Bombylius major** L.

Flowers visited: *Antennaria neglecta.* White.
Rudbeckia hirta. Yellow.
Anthemis Cotula. White.
Arctium Lappa. Purple.
Sanguinaria canadensis. White.
Claytonia virginica. Reddish.
Hepatica acutiloba. Purplish.
Caltha palustris. Yellow.
Ranunculus septentrionalis. Yellow.
Vicia caroliniana. Bluish.
Cardamine Douglassii. Purplish.
Prunus nigra. White.
Isopyrum biternatum. White.
Salix rostrata. Yellow.

Alltogether for the 14 flowers:

White and yellow 64.3%.
Red, purple and blue 35.7%.

5. **Systœchus vulgaris** Loew.

Flowers visited: *Eupatorium purpureum.* Purple.
Solidago juncea. Yellow.
Heliopsis scabra. Yellow.
Helianthus strumosus. Yellow.
Verbena hastata. Blue.
Blephilia hirsuta. White.
Melilotus alba. White.
Monarda fistulosa. Purplish.
Teucrium canadense. Reddish.

Alltogether for the 9 flowers:

White and yellow 55.6%.
Red, purple and blue 44.4%.

6. **Sparnopolius fulvus** Wied.

Flowers visited: *Aster paniculatus.* White.
Aster Drummondii. Blue.
Aster puniceus. Blue.
Aster nova-angliæ. Purple.

Eupatorium urticaefolium. White.
Solidago canadensis. Yellow.
Solidago graminifolia. Yellow.
Rudbeckia hirta. Yellow.
Helianthus strumosus. Yellow.
Helianthus giganteus. Yellow.
Helenium autumnale. Yellow.
Grindelia squarrosa. Yellow.
Bidens laevis. Yellow.

Alltogether for the 13 flowers:
White and yellow 76.9%.
Purple and blue 23.1%.

7. **Exoprosopa decora** Loew.

Flowers visited: *Aster puniceus.* Blue.
Aster nova-angliae. Purple.
Solidago juncea. Yellow.
Heliopsis scabra. Yellow.
Rudbeckia laciniata. Yellow.
Helianthus strumosus. Yellow.
Verbena hastata. Blue.

Alltogether for the 7 flowers:
Yellow 57.1%.
Purple and blue 42.9%.

8. **Exoprosopa fascipennis** Say.

Flowers visited: *Aster furcatus.* White.
Eupatorium perfoliatum. White.
Eupatorium purpureum. Purple.
Rudbeckia laciniata. Yellow.
Helianthus strumosus. Yellow.

Alltogether for the 5 flowers:
White and yellow 80.0%.
Purple 20.0%.

9. **Exoprosopa fasciata** Macq.

Flowers visited: *Eupatorium perfoliatum.* White.
Eupatorium purpureum. Purple.
Liatris spicata. Reddish.
Verbena hastata. Blue.

Alltogether for the 4 flowers:

White 25.0%.

Red, purple and blue 75.0%.

The percentages for the same species of Bombylids as derived from Robertson's data for southern Illinois are as follows:

1. **Anthrax alternata.** (6 flowers). White etc. 100%.
   Red etc. ——
2. **Anthrax halcyon.** (12 flowers). White etc. 100%.
   Red etc. ——
3. **Bombylius fulvibasis.** (6 flowers). White etc. 16.7%.
   Red etc. 83.3%.
4. **Bombylius major.** (11 flowers). White etc. 72.7%.
   Red etc. 27.3%.
5. **Systœchus vulgaris.** (24 flowers). White etc. 54.2%.
   Red etc. 45.8%.
6. **Sparnopolius fulvus.** (21 flowers). White etc. 90.5%.
   Red etc. 9.5%.
7. **Exoprosopa decora.** (7 flowers). White etc. 85.7%.
   Red etc. 14.3%.
8. **Exoprosopa fascipennis.** (12 flowers). White etc. 83.3%.
   Red etc. 16.7%.
9. **Exoprosopa fasciata.** 20 flowers). White etc. 40.0%.
   Red etc. 60.0%.

From these figures for the 9 species of bee-flies under consideration we obtain the following average for each locality:

	White and yellow.	Red, purple and blue.
Milwaukee, Wis.	66.1%	33.9%
Carlinville, Ill.	71.5%	28.5%

Several other species of Bombylids have been observed as flower-visitors in Milwaukee Co., and for the sake of completeness I add a list of these, together with the flowers visited:

Spogostylum albofasciatum Macq. visiting *Monarda fistulosa.*

Spogostylum œdipus Fabr. visiting *Eupatorium urticaefolium.*

Aldrichia ehrmanni Coq. visiting *Erigeron philadelphicus.*

Anthrax fulviana Say. visiting *Aster paniculatus, A. puniceus* and *Solidago canadensis.*

Anthrax lateralis Say. visiting *Ceanothus americanus.*

Anthrax parvicornis Loew. visiting *Verbena hastata.*

Anthrax sinuosa Wied. visiting *Solidago juncea, Tofieldia glutinosa* and *Monarda fistulosa.*

Phthiria punctipennis Walk. visiting *Eupatorium perfoliatum, Heliopsis scabra, Rudbeckia hirta, R. laciniata* and *Helianthus strumosus.*

Geron calvus Loew visiting *Rudbeckia hirta.*

In this account alltogether 18 species of bee-flies figure as visitors to 52 species of flowers, which latter represent the following 17 families:

1. **Liliaceæ.** *Tofieldia glutinosa.*
   Allium canadense.
   Smilacina racemosa.
2. **Salicaceæ.** *Salix rostrata.*
3. **Caryophyllaceæ.** *Stellaria longipes.*
4. **Portulacaceæ.** *Claytonia virginica.*
5. **Ranunculaceæ.** *Ranunculus septentrionalis.*
   Hepatica acutiloba.
   Isopyrum biternatum.
   Caltha palustris.
6. **Papaveraceæ.** *Sanguinaria canadensis.*
7. **Cruciferæ.** *Cardamine Douglassii.*
8. **Saxifragaceæ.** *Parnassia caroliniana.*
9. **Rosaceæ.** *Prunus nigra.*
10. **Leguminosæ.** *Melilotus alba.*
    Vicia caroliniana.
11. **Anacardiaceæ.** *Rhus glabra.*
12. **Rhamnaceæ.** *Ceanothus americanus.*
13. **Umbelliferæ.** *Cicuta maculata.*
    Sium cicutafolium.
    Pastinaca sativa.
    Oxypolis rigidior.
    Angelica atropurpurea.
14. **Verbenaceæ.** *Verbena hastata.*
15. **Labiatæ.** *Teucrium canadense.*
    Monarda fistulosa.
    Blephilia hirsuta.
16. **Caprifoliaceæ.** *Viburnum dentatum.*

17. Compositæ. *Eupatorium purpureum.*
Eupatorium perfoliatum.
Eupatorium urticæfolium.
Liatris spicata.
Grindelia squarrosa.
Solidago juncea.
Solidago canadensis.
Solidago graminifolia.
Aster furcatus.
Aster novæ-angliæ.
Aster Drummondii.
Aster paniculatus.
Aster puniceus.
Erigeron philadelphicus.
Antennaria neglecta.
Heliopsis scabra.
Rudbeckia hirta.
Rudbeckia laciniata.
Helianthus strumosus.
Helianthus giganteus.
Bidens lævis.
Helenium autumnale.
Anthemis Cotula.
Arctium Lappa.

According to this list we are dealing with 37 white and yellow flowers (about 71%) as against 15 red, purple and blue (about 29%), in other words more than twice as many white and yellow flowers have received the attention of these flies than red, purple and blue ones, and this is just the opposite of what H. Mueller found. These figures taken in connection with those given for the 9 species of Bombylids which were considered separately justify the conclusion, that these flies do not show a preference for any particular color. *Bombylius fulvibasis*, for example furnishes at Milwaukee a much greater percentage of visits to white and yellow flowers, while the same insect was seen at Carlinville, Ill. on a greater number of red, purple and blue flowers.

Quite recently Langhoffer[3] published the results of his observations on the visits of two European species of *Bombylius: B. discolor* and *B. fuliginosus.* These observations cover a period of

3) A. Langhoffer Bluetenbiol. Beobacht. an Dipteren. Zeitschr. f. Wissensch. Insektenbiol. Vol. VI, pp. 14-17 and 57-61 (1910).

7 years, and show that *B. discolor* is a very regular visitor of *Pulmonaria officinalis (Boraginaceæ)*, and that it prefers the flowers of this to those of any other species, visiting other flowers in the case of necessity only. In *Pulmonaria officinalis* a change of color takes place from red in the younger to blue in the older flower, and *Bombylius discolor* is seen to favor the red flowers and spend more time at them for the simple reason, as Langhoffer states, that they contain more nectar than the blue ones. In the case of *Bombylius fuliginosus* this author noticed a preference for the blue tubular flowers of *Muscari neglectum (Liliaceæ)*.

In our region *Bombylius major*, the earliest of our Bombylids flies from about the 26th of April to the end of July. During the first few weeks of its period of flight it may be seen at the white flowers of *Antennaria neglecta*, *Prunus nigra* and *Sanguinaria canadensis* (the latter a so-called pollen-flower, one in which no nectar is secreted), the yellow flowers of *Caltha palustris*, *Ranunculus septentrionalis* and *Salix rostrata* (probably also on some other species of *Salix*), the red flowers of *Claytonia virginica*, and the violet flowers of *Vicia caroliniana*, *Cardamine Douglassii* and *Hepatica acutiloba*, the latter also a pollen-flower.[4]) It is a rather frequent visitor at the red flowers of *Claytonia virginica*, without however showing a decided preference for this species.

Structure of the flower, odor, taste and supply of nectar determine probably more than anything else the extent to which a flower is attractive to such an insect. As stated above Langhoffer explains the more frequent and longer visits of *Bombylius discolor* to the younger red flowers of *Pulmonaria* as being due to the greater amount of nectar contained in these than in the older blue flowers. If we could change the color of such a flower to white or yellow without changing its structure and the odor and taste of its nectar there is hardly any reason to doubt, that it would prove as attractive to *Bombylius discolor* as otherwise. The same may be said for the blue flower of *Muscari neglectum* in its relation to *Bombylius fuliginosus*.

II. FLOWERS VISITED BY SHORT-TONGUED BOMBYLIDS.

For the short-tongued species belonging to the genera *Lomatia*, *Anthrax* and *Argyramœba (Spogostylum)* it has been

4) Regarding pollenflowers and Bombylids we have the following in Knuth's Handbook, Vol. 1, p. 183: "The species of *Bombylius* like those of *Empis* are also able to bore into succulent tissues." Further on, following a discussion of the anatomy of the mouthparts we read: "I have often seen species of *Bombylius* thrust their proboscis into nectarless flowers (e. g. *Bombylius canescens* Mik into *Hypericum perforatum*), and I imagine that here the boring apparatus was brought into action."

claimed, as mentioned above, that they exhibit a decided preference for flowers with exposed nectar.

A glance at the list of flowers visited by *Anthrax alternata* shows that 7 of these belong to the type with exposed nectar, while in the remaining 5 (4 *Compositæ* and *Verbena hastata*) the nectar is concealed. Of the 6 flowers visited by the same insect at Carlinville, Ill., only 1 has exposed nectar (*Euphorbia corollata*).

For *Anthrax halcyon* we find all of the flowers visited at Milwaukee as well as at Carlinville belonging to the *Compositæ*, *i. e.* with concealed nectar. In those figuring in the Milwaukee list the nectar is concealed at the bottom of tubes ranging in length from 1 mm.,[5] as in *Eupatorium perfoliatum* and the 2 species of *Solidago*, to 4 or 4.5 mm. (*Eupatorium purpureum* and *Helianthus strumosus*).

In the case of the 4 additional species of *Anthrax* referred to above (*fulviana*, *lateralis*, *parvicornis* and *sinuosa*) only 1 of the species of flowers visited (*Toficldia glutinosa*) has exposed nectar.

As to *Spogostylum* (of which *Argyramœba* mentioned by Knuth is a synonym) *Monarda fistulosa* visited by *S. albofasciatum*, and *Eupatorium urticæfolium* visited by *S. œdipus* are both flowers with concealed nectar.

Summing up our results for the 6 species of *Anthrax*, and the 2 species of *Spogostylum* observed at Milwaukee we note that among the 31 species of flowers visited 8 or only 26% have exposed nectar. The statement that the short-tongued bee-flies belonging to the genera *Anthrax* and *Spogostylum* (*Lomatia*, the third genus referred to in this connection in Knuth's Handbook does not occur in our region) prefer flowers with exposed nectar does not hold good for our region.

III. RELATIONS OF BOMBYLIDS TO SOCIAL FLOWERS.

The *Compositæ* are the most important among the so-called social flowers. In the temperate regions of our North American continent they occupy a prominent position in the make-up of the flora. In the latest list of the flora of Milwaukee County published by Mr. Howland Russel[6] 921 species of ferns and flowering plants are enumerated, and the *Compositæ* figure in this list with 152 species or 16.5% of the flora. Data obtained from specimens in the herbarium of the Public Museum of Milwaukee, as

5) S. Graenicher: Wisconsin flowers and their pollination. Compositae. Bull. Wis. Nat. Hist. Vol. VII. pp. 19-77. (1909).

6) Howland Russel, Check list of the flora of Milwaukee County. Bull. Wis. Nat. Hist. Soc. Vol. V, pp. 167-250 (1907).

also notes of my own have enabled me to construct a flowering curve for 122 of our species of *Compositæ*. Some time in April or around the beginning of May, according to meteorological conditions, the flowers of the earliest species, the dandelion make their appearance, followed a few days later by *Antennaria neglecta*. During the first half of May two other species of *Antennaria* begin to bloom, towards the end of the month two species of *Erigeron* and one of *Senecio* arrive on the scene, and we notice a gentle rise of the curve up to the beginning of July, from which time on a very rapid rise leads to a maximum around the end of August. From there on a more or less gradual decline is noticeable, and the flowering season is, as a rule cut short by the appearance of a severe frost around the end of October or the beginning of November. According to the available data only 18 of the 122 species considered appear before the 1st. of July, the bulk of the family is therefore made up of summer and fall bloomers.

This curve agrees quite closely with the curve presented by Robertson[7] for Carlinville, Ill.

Judging from the enormous number of individuals by which these plants are represented in our flora we are led to consider this type of floral structure a very successful one, one possessing a rather favorable combination of characters. It is therefore not surprising to learn that these flowers prove very attractive to the flower-visiting insects, and that in some instances the relations between flower and insect are quite close. Robertson[8] in referring to the most important visitors of the *Compositæ* includes the Bombylids and gives a flight curve for this family, according to which the greatest number of species is on the wing from about the middle of June to the end of August when the maximum is reached. A corresponding curve for the *Bombyliidæ* of Milwaukee Co., based on observations covering 22 species has its starting point near the end of April, rises slowly to the beginning of July, and from there takes a rapid spurt upwards to a maximum lasting throughout the month of August. This curve bears much resemblance to the flowering curve of the *Compositæ*.

In the list of flowers for which the visits of Bombylids have been recorded, and which are arranged according to families (p. 95) 24 out of the 52 species or 46% belong to the Compositæ. If we consider the number of flowers visited by each of the 18 species of Bombylids referred to in this paper, we have out of a

7) Chas. Robertson. The philosophy of flower seasons etc. Am. Nat. Vol. XXIX, pp. 97-117 (1895).
8) Chas. Robertson. Loc. cit. p. 110.

totality of 94 visits 60 credited to species of *Compositæ,* and this amounts to 64% in favor of these flowers. These figures prove rather conclusively that, so far as the relations of the bee-flies to social flowers are concerned, the statement that the latter are very rarely visited by the former does not apply to the temperate regions of our continent.